

Polymorphism in an ant mimic

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Abstract.

Myrmarachne bakeri Banks 1930 is a polymorphic, generalized ant-mimicking jumping spider. In this study, variation in its polymorphic characters was observed and described. *Myrmarachne bakeri* varies in color, glossiness and patterns, and differs from other polymorphic ant-like spiders because it becomes polymorphic before adulthood. Morphological changes appear to have no set archetype and few spiders revert to morphs previously observed. Polymorphism is widespread in *Myrmarachne* but to date no species has been shown to exhibit the variation found in *M. bakeri*.

Spider coloration is typically seen as a result of selection by visually-hunting predators (Oxford & Gillespie 1998). Apostatic selection occurs when a given phenotype is under-represented in a predator's diet when it is rare but is over-represented when it is above a threshold abundance (Ruxton et al. 2004). This type of selection favors rarer morphs and may lead to polymorphism in characters recognized by the predator.

Many spiders are myrmecomorphic (ant-like) and, through their resemblance to ants, gain protection from predators that normally avoid ants because ants are dangerous and heavily defended (Nelson & Jackson 2006). This phenomenon, known as Batesian mimicry, in this case of ants, is especially common in the Salticidae (Cushing 1997). Several myrmecomorphic salticids are polymorphic (e.g., Oliveira 1988; Ceccarelli & Crozier 2007), but polymorphism can adopt various forms. Transformational mimics are those that change morphology at different instars, with each morph resembling a particular model (see Cushing 1997). Other myrmecomorphs are polymorphic as adults and seem to have one particular model for each morph, while in other cases adults are sexually dimorphic and each sex mimics a different model (Oliveira 1988; Cushing 1997).

All species of *Myrmarachne* are Batesian mimics of ants (Edmunds 1993; Nelson & Jackson 2006; Nelson et al. 2006). *Myrmarachne*, like most salticids, are cursorial predators and rely primarily on vision to hunt their prey and to communicate with conspecifics (Richman & Jackson 1992; Nelson & Jackson 2007). Adults of the species studied here, *Myrmarachne bakeri*, do not appear to have any particular ant model; instead appearing to be generalized ant mimics. My first impression was that it was sexually dimorphic (like all species of *Myrmarachne*, adult males of *M. bakeri* have elongated chelicerae), with each sex having two morphs, a “red” morph (Fig. 1A,B) and a “black” morph (Fig. 1C,D), leading me to believe that they mimicked two different ant models, one red and one black. However, it soon became clear that instead of simply having two distinct morphs, color variation in *M. bakeri* covers a whole spectrum of patterns, which I describe here.

I collected large juvenile and adult spiders in the vicinity of the International Rice Research Institute (IRRI) at Los Baños in the Philippines and housed them at IRRI and in the School of Biological Sciences at the University of Canterbury, New Zealand. Spiders were maintained in individual plastic cages, cleaned weekly, with a cotton roll through the bottom that dangled in a small cup of water, providing humidity. All spiders were fed twice a week. Spiders less than 3 mm were fed wild-caught white flies, and cultured *Drosophila* and small cultured house flies (*Musca domestica*) thereafter.

After collection, adult sex was noted and juveniles labeled as such. Spiders were then described in detail and sketched, paying particular attention to the spider's abdomen, as it was the abdomen that varied most. In descriptions of dermal morphology, "shiny" denotes that the spider glistened in the artificial light in the laboratory and did not have a 'hairy' or 'furry' appearance while "dull" spiders did not glisten and had a 'hairy' or 'furry' appearance. Ventrally, *M. bakeri* exhibited changes of glossiness and darkening or lightening of parts, or all, of the abdomen. However, five individuals (4.8%) developed a ventral line along the sagittal plane. Morphs were considered different when there were visible changes in the colors on the dorsal side of the abdomen or changes in the number, or thickness, of dorsal abdominal lines. I did not consider a darkening of coloration after molting a different morph, as this may have been the product of the hardening of the exoskeleton.

Each time a spider was checked, described, and re sketched, the cage was cleaned. I checked all spiders daily for molting, as evidenced by the exoskeleton in the cage. Each time a molt was found this was noted, along with any morphological changes in the spider. Regardless of whether molting had occurred, each spider was described every three weeks until it died. In total, 105 spiders (70 females and 35 males) were described from collection until death, in many cases 6 months later.

Individual spiders changed in glossiness and markings. Surface glossiness, in which the individual appeared shiny sometimes and dull other times, changed in 17 (16.19%) individuals. Regardless of color, individuals might be shiny or dull (Fig. 1A,E), although more than 80% of black

spiders were dull (Fig. 1C). Four spiders (3.81%) developed two white spots above the anterior medial eyes (Fig. 1F). These spots (termed ‘eye spots’) developed in both sexes and occurred in individuals of different colors. Once eye spots developed, they did not disappear, despite changes in overall coloring of the spider. Fourteen females (20%) developed black triangles on the sides and occasionally the middle of the abdomen, towards the anterior end. In three individuals these triangles joined over time and became a new line on the abdomen. These triangles were always observed on the dorsal side of the abdomen (Fig. 1G,H).

Additionally, *M. bakeri* exhibited both color changes and polymorphism, although only four males (11.4%) changed morph once they became sexually mature adults (Fig. 1B,D,I,J). The chelicerae and cephalothoraces of males were black or dark red, although the cephalothorax and the chelicerae were not necessarily the same color (Fig. 1D,K). Overall, *M. bakeri* exhibited a large variety of colors that were expressed uniformly or in combination at some stage in their lives. These colors included light to dark red (74.2%; Fig. 1L,M,N,O), orange (36.19%; Fig. 1P,Q), yellow and gold (26.7%; Fig. 1H,R,U), ochre (1%), brown (40%; Fig. 1G,S), black (94.3%; Fig. 1C,T), and white (26.7%).

Most spiders (79.4%) changed morphs throughout the six-month observation period (Fig. 1K & V, B & J, I & P, A & L). From the total pool of spiders (N = 105), 28.9% exhibited two morphs, 25.8% exhibited three, 13.4% four, 8.3% five and 3.1% exhibited six different morphs. Spiders that went through three morphs or more were checked to see whether they had reverted to a previous morph. Just over a quarter of these (26.4%) were found to have reverted to a previous morph. Consequently, in *M. bakeri*, it appears that polymorphism occurs both between and within individuals. Furthermore, *M. bakeri* continued to change morphologically throughout the six-month period in the laboratory, where the feeding regime, as well as light, humidity, and temperature were controlled, suggesting that this polymorphism is not merely environmentally conditioned, and presumably has a genetic basis. Further research on the genetics underlying polymorphism in mimicry (Ceccarelli & Crozier 2007) may yield particularly interesting results.

Polymorphism in the Hawaiian happy-face spider (*Theridion grallator* Simon, 1900) is controlled at one, or sometimes more, loci (depending on the island) (reviewed in Oxford & Gillespie 1998). In general, within patterned morphs, these spiders appear to have dominance of some alleles which are superimposed on the area of pigmentation controlled by another allele. Although in *M. bakeri* there are several morphs throughout life, a close look at the spiders does suggest what may be pattern superimposition. For example, some markings appear superimposed on others, such as the red 'spots' on the anterior of the abdomen (Fig. 1M,N,Q,T). Another analogy can be made between *T. grallator* and *M. bakeri*: both exist in volcanic archipelagos in which the possibility of population differentiation and speciation are particularly marked when compared to the mainland due to random events such as a volcanic eruption.

Four virgin females were allowed to mate and were then observed at a later stage with eggsacs that hatched into spiderlings. This strongly suggests that they belonged to the same species as the males. However, *Myrmarachne* are notoriously difficult to rear in laboratory conditions and the viability of the offspring could not be tested, as it was impossible to rear the young to adulthood. Nevertheless, all spiders that hatched were monitored until death. During the first two or three instars spiders exhibited only one morph (ant-like) consisting of a translucent body with a single black line on the abdomen. The subsequent 2 or more instars were also monomorphic, but consisted of a pale orange body with no lines or other markings (termed 'juvenile' morph). This suggests that *M. bakeri* has one particular ant model for each of these two morphs and that this may be a case of transformational mimicry, in which different morphs at different life stages resemble distinct ant models (Cushing 1997). However, due to the inability of successfully rearing any individual through all instars into adulthood I was unable to determine how many instars are monomorphic (for either the early instar morph or the juvenile morph) and at what stage polymorphism within and between individuals occurs. However, a few individuals collected as large juveniles in the field became polymorphic three instars short of sexual maturity, with individuals exhibiting several different morphs. Overall, individuals

changed morphology up to six times and few individuals had the same colors and patterns, suggesting that molting may not be a prerequisite to induce morphological changes in this species. While these results are merely suggestive, this aspect of *M. bakeri*'s polymorphism seems a particularly interesting avenue for further investigation.

Palatable Batesian mimics exploit the predator's aversion by evolving similar coloration to that of distasteful or dangerous animals, requiring them to be less numerous than the model. This frequency-dependant selection occurs because predators must encounter the unpalatable model more often than the palatable mimic in order to learn (or evolve, on a greater time scale) characteristic cues of the model and thereby avoid them (Ruxton et al. 2004; Nelson & Jackson 2006, Nelson et al. 2006).

Some animals, such as spiders and mantids, have an innate fear of ants (Nelson & Jackson 2006, Nelson et al. 2006). Just as in learned aversion, mimics that resemble models for which animals have evolved an innate fear may also benefit from being polymorphic. There must be considerable selection to maintain innate fear of dangerous prey and if there are many benign mimics, this pressure may be slackened. However, as with learned aversion, polymorphism (in the mimic) reduces the apparent number of the mimics per model and therefore the selective pressure for aversion of the model is maintained because the characteristics of the prey continuously change and therefore predators may not develop innate mechanisms whereby they can distinguish the palatable mimic from its unpalatable model. Consequently, polymorphism is often expected among Batesian mimics (Ceccarelli & Crozier 2007) and may provide a selective advantage through an apparent reduction in the frequency of the mimic relative to the model (Oliveira 1988; Ritland 1995). This idea assumes that it is beneficial to parents to spread genes of different morphs so offspring do not appear common and are therefore not easily 'targeted' by predators. Indirect evidence for the possibility that polymorphism is selected for by (visual) predators lies in the marked difference between the observed polymorphism on the dorsal and ventral sides of the abdomen in *M. bakeri*. Predators would rarely view the spider from its ventral surface and therefore there would be little point in extending polymorphic characters

ventrally.

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FIGURE LEGENDS

Figure 1.- Polymorphism in *Myrmarachne bakeri*. Photos courtesy of Robert Jackson. (A) ‘Red’ female (c.f. L, same individual); (B) Shiny red male (c.f. J, same individual); (C) Shiny black male; (D) Shiny red female; (E) Dull ‘black’ female; (F) Black, shiny male with whitish eyespots; (G) Brown female with triangles on the anterior part of the abdomen; (H) Female with yellow abdominal tip and triangles at the anterior of her abdomen; (I) Pale red male (adult of spider in P); (J) Male with dark red coloration (c.f. B, same individual); (K) Red male with black chelicerae (adult of spider in V); (L) Dark red female (c.f. A, same individual); (M) Red female (eating *Drosophila*). Note what may be pattern superimposition; (N) Red female. Note what may be pattern superimposition; (O) Red female; (P) Orange subadult male (eating *Drosophila*) (adult is shown in I); (Q) Orange female (eating *Drosophila*). Note what may be pattern superimposition; (R) Yellow female; (S) Brown female (eating *Drosophila*); (T) Orange, red, and black female (eating *Drosophila*). Note what may be pattern superimposition; (U) Female (eating *Drosophila*) with a golden abdominal tip; (V) Shiny subadult male (eating *Drosophila*) (adult is shown in K).